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NEW DIMORPHIC MUTANTS OF THE OENOTHERAS

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(WITH FIVE FIGURES)

Among the previously described mutants of *Oenothera Lamarckiana* Ser. there is a form which, although fertile with its own pollen, yields a dimorphic progeny. Some of the individuals exactly repeat the stature and characters of their parent, but others return to the type of *O. Lamarckiana*. Besides these, new mutants, especially *O. oblonga*, are relatively numerous. The two main types are produced in varying proportions, according to the individual cultures. The typical specimens may be as few as 10 per cent, or as numerous as 80 per cent. In most instances, however, they show a proportion of about 35-40 per cent. Considering the much smaller individual strength of the typical ones, as compared with the atavistic specimens, these figures may be regarded as indicating a splitting, ordinarily, into nearly equal parts.

This inconstant mutant is *O. scintillans*.¹ Exactly the same phenomenon of splitting has been observed recently in a number of new types. In the first place, in *O. stenomeres* mut. *lasiopetala*, described by BARTLETT.² In the second place, it has occurred in my own cultures, among the new mutants of *O. Lamarckiana*, as well as among those of another American species, described under

¹ The mutation theory. Chicago. 1909. Vol. I, p. 377; and Gruppenweise Artbildung, p. 257. 1913.

² BARTLETT, H. H., Mutations of *O. stenomeres*. Amer. Jour. Bot. 2:100-109; see also 2:146. 1915.

the preliminary name of *O. biennis* Chicago.³ I shall deal with this one under the name *O. saligna*, and designate the new inconstant mutants of *O. Lamarckiana* as *O. cana*, *O. pallescens*, *O. Lactuca*, and *O. liquida*. As far as investigated, they all follow the rule that in every generation they split up into two ordinarily almost equal groups of typical specimens and of atavistic individuals which, in all cases, exactly duplicate the characters of *O. Lamarckiana*.⁴ Moreover, they show a relatively high degree of mutability.

With one of them, *O. cana*, I have made a number of crosses with allied forms, in order to ascertain that it behaves in the same manner as *O. scintillans*, and that the same conception of heterogamy must be applied here also. In this mutant the pollen carries only the hereditary qualities of *O. Lamarckiana*, and the specific marks of the mutant are handed down to their progeny through the ovules only.⁵ This conception of heterogamy may be considered to hold good for the other inconstant types also.

The same behavior is found in *O. lata*, but since this form never produces any fertile pollen in my cultures and has to be fertilized by *O. Lamarckiana* in order to produce seeds, the evidence which it affords is less stringent than that given by the self-fertile dimorphic races.

Oenothera Lamarckiana mut. *cana*.—Among a number of dubious mutants from *O. lata* which were cultivated as biennials in 1906–1907, a plant was noticed in the third generation of that family with narrower leaves of a gray color, evidently constituting a new type. It was very vigorous, reached a height of about 2 m., and was self-fertilized. It will be designated as *O. cana* from *lata* no. 1, since the first family of *O. cana* was derived from it.

Next year the same mutant type was recognized among the young rosettes, issuing from different samples of seeds of *O. lata* (fig. 1). All in all there were 5 specimens of *O. cana*. In order to determine the frequency of this mutant I have made two cultures

³ Gruppenweise Artbildung, p. 52. fig. 18 and pl. 6. 1913.

⁴ In the wild condition such a splitting would evidently cause a race to die out after a few generations, especially since the atavists are very fertile and much stronger than the mutant form. As a matter of fact, inconstant wild species of this type are not known. See The mutation theory, Vol. I, p. 380.

⁵ Gruppenweise Artbildung, p. 273. 1913.

on a sufficiently large scale, using the seeds produced by my pure strain of *O. lata* fertilized by *O. Lamarckiana*. The seeds of 1909 gave 564 seedlings, with 18 per cent *lata* and 2 per cent *cana*. Those of 1908 gave 1550 seedlings, 8 per cent of which were *lata* and 9 per



FIG. 1.—*Oenothera Lamarckiana* mut. *cana*: a young plant showing the narrow leaves by which it is easily distinguished from rosettes of the *Lamarckiana* type in the same sowings; June 11, 1915.

cent were *cana*. Other mutants appeared in these cultures in different proportions, as usual.

Among the seeds of pure *O. Lamarckiana*, *O. cana* is much the rarer. In 1913 I fertilized, on 5 strong biennial specimens, almost all the flowers during two months and got sufficient seed to have 20,000 seedlings in 1914. Of these only 6 were *cana*, giving a percentage of 0.03 per cent. In the same boxes 7 *rubrinervis* and 5

scintillans appeared as mutants, showing that the mutation coefficients for these three forms do not essentially differ from one another.

Stray mutations into *cana* have appeared in later years in different cultures, as, for instance, in 1913 in those of *O. laevifolia* and *O. scintillans*. Three mutations from *O. pallescens* will have to be recorded in the pedigrees relating to this form. It seems probable that *cana* mutants also have appeared in previous years, but have not been distinguished from other narrow-leaved types, of which there have always been quite a number in the larger cultures. Many other mutations also have escaped observation during a series of years until a single specimen developed into a strikingly new type.

I have cultivated *O. cana* mostly as annuals, but in some instances as biennials. In both cases the stature is the same as that of *O. Lamarckiana*, but in the annuals the stems are slender and the foliage rather loose, whereas the biennials have thick and strong stems with dense foliage. The leaves are narrow, with a shorter blade and a longer petiole, and of a very striking gray color. The flower buds are long and thin, contrasting sharply with those of *O. Lamarckiana* and even more so with those of *O. pallescens* and *O. Lactuca*. The spike is less dense than in the parent species and the fruits are more cylindrical and narrower, containing fewer seeds (fig. 2). In the flowering condition, as well as in the stage of young rosettes, the plants are now easily recognized, but at other periods of their development it is often difficult to identify and count them, some specimens showing their marks very clearly, but others resembling more or less their *Lamarckiana*-like sisters.

The easiest marks are afforded by the flower buds. Measured the day before opening and with the tube and ovary, their size varies, as a rule, from 75–80 mm., against 80–95 mm. in *O. Lamarckiana* cultivated under the same conditions; means 77.5 against 90 mm. The breadth, measured at the base of the conical part above the tube, is only 7 mm. The 4 tips at the top of the bud are more or less bent on one side, and this curious mark is so striking that it is often the first which draws the attention to a stray mutant of the *cana* type (fig. 2). The 4 lobes of the stigma are

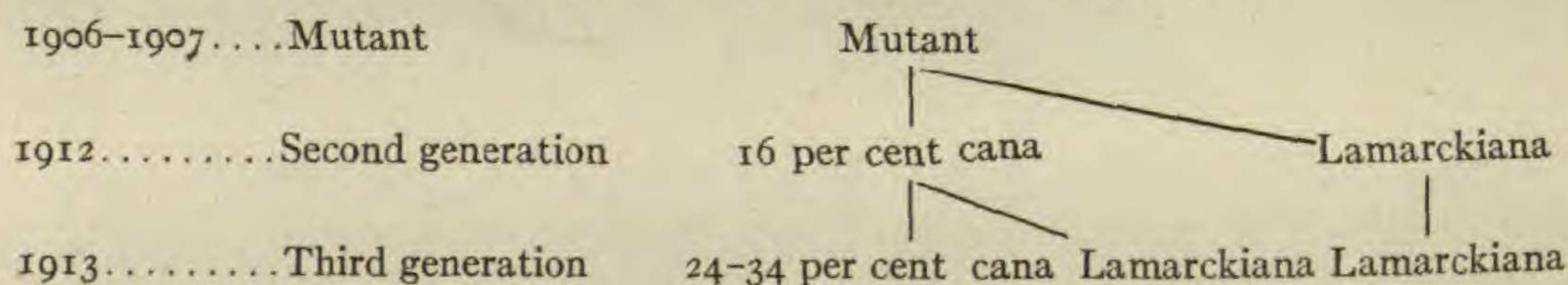


FIG. 2.—*Oenothera Lamarckiana* mut. *cana*: flowering spikes of the two types into which each generation splits; on the left the *Lamarckiana* type, on the right the parental type, showing the thin buds and the bent tips of the calyx; the difference in height of the 2 spikes is the same as the mean difference in height of the 2 groups on the bed; third generation of mut. *cana* no. 3, photographed July 22, 1914.

more slender than in *O. Lamarckiana*; the anthers are thin, provided with a good supply of pollen on stout specimens, but often deficient in this production on the weaker ones, especially in annual cultures.

O. Lamarckiana mut. *cana*.—Among the *cana* mutants from *O. Lamarckiana* only one specimen has been self-fertilized. It arose in 1913 in the fourth guarded generation from a plant introduced into my garden in 1905 from the original field near Hilversum. It was only recognized at the end of July, when it opened its first flowers. It yielded few seeds, which gave rise to 19 seedlings only, all of which flowered in 1914. Of these, 13 exactly duplicated the type of *O. Lamarckiana*, 5 were *cana*, and one was a mutant *nanella*. These figures point to a percentage of 26 per cent *cana*.

O. cana from *lata* no. 1.—From the first mutant of 1906–1907, previously described, I have derived a pedigree family in order to try its constancy and got the following result:



The size of these cultures is given in table I.

TABLE I

YEAR	GENERATION	PARENT	OFFSPRING		PER-CENTAGE OF CANA	MUTANTS
			Total	Flowering		
1912.....	Second	mutant	31	30	16
1913.....	Third	<i>cana</i>	49	48	24	1 <i>nanella</i>
1913.....	Third	<i>cana</i>	115	65	34	4 <i>nanella</i>
1913.....	Third	<i>Lamarckiana</i>	60	25	0

The offspring of two *cana* individuals of the second generation have been studied separately, as well as those of one specimen of the *Lamarckiana* type. The plants have been under observation through their whole lifetime, so far as space allowed, the numbers of the flowering individuals being given in the column next to that of the totals. The *cana* were all of the same type; the *Lamarckiana* exactly repeated the marks of the original species. Three of the dwarfs have flowered. They all had the marks of ordinary *O. La-*

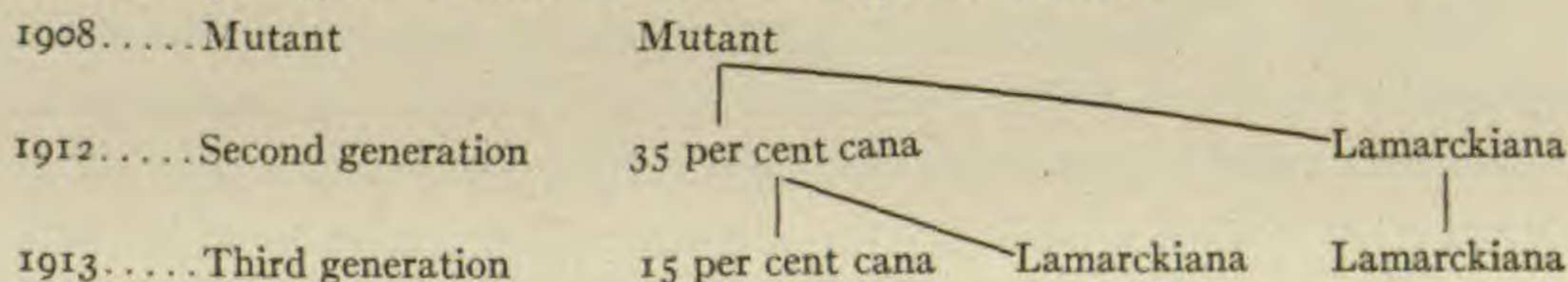
marckiana mut. *nanella* and none of those of *O. cana*. This has been the case in some of the other pedigree cultures of this type, but it should be remarked that in other cases the characters of *O. cana* may combine with the dwarf stature. Such dwarfs have the narrow gray foliage and are easily distinguished from typical *O. nanella* specimens.

The self-fertilized seeds of the *cana* individuals split in both generations into *cana* and *Lamarckiana*, just as *O. scintillans* splits into *scintillans* and *Lamarckiana*. The proportions 16-24-34 per cent with a mean of 25 per cent seem to indicate a splitting into nearly equal parts, with a loss on the side of the weaker form. The same deviation from equality will be seen in almost all the figures of this article, and the same explanation must be considered as applying to all of them. It is almost always the new type which is in the minority.⁶

The seeds of the *Lamarckiana*-like individuals do not give rise to a splitting of this kind, keeping true to their parent form. The same fact recurs in all the pedigrees to be mentioned later on, and for all the new dimorphic types. It may be taken to be the rule, therefore, although the trials have been only one or two in each instance. It agrees fully with the behavior of the analogous splitting products of *O. scintillans*.

O. cana from *lata* nos. 2 and 3.—In a culture of about 600 seedlings of *O. lata*, 4 mutants of the *cana* type arose in 1908. The *lata* strains had been derived from some annual mutants which had been produced by my *O. Lamarckiana* in 1905, and described in my *Gruppenweise Artbildung* (p. 247). From these mutants a second generation was cultivated in 1907, and fertilized by the pollen of *Lamarckiana*-like individuals of the same culture. Their seeds yielded the two *cana* mutants to be described here, and two others, from the seed of which only one generation has been studied.

The pedigree of mutant no. 2 is given below:



⁶ Excepting the case of biennials; see later statement.

the percentage figures come so much nearer to equality of the two types than in the other cases is probably owing to this striking vigor of the race. The means are 25 per cent *cana* for no. 1 and no. 2, but 53 per cent *cana* for no. 3. The proportion of mutants among the seedlings of the *cana* individuals is 18 in 350, or about 5 per cent.

O. cana from *lata* nos. 4 and 5.—As previously mentioned, the progeny of two further mutants of the same origin have been studied. The offspring of one of them embraced only 15 individuals, of which 13 have flowered. There were 3 *cana*, 2 mutants (one *oblonga* and one of the same new type as in no. 2), the 10 remaining plants being externally like *O. Lamarckiana*. The second original mutant yielded only 11 offspring, among which 7 were *cana*, one *Lamarckiana*, and 3 *oblonga*. Although these cultures do not justify the calculation of percentage figures, they evidently support the conclusions drawn from the three former ones, and argue for the conception that this form of splitting is typical for *O. cana*.

INFLUENCE OF CULTURE ON PERCENTAGE FIGURES.—I have shown⁷ that the percentage figures for the splitting of *O. scintillans* in the succeeding generations may differ for different families. Sometimes it is only 15 per cent, more often it varies between 34 and 39 per cent, and in rare cases it reaches 69–93 per cent. Subsequent experiences have suggested the idea that these differences are due mainly to outward conditions or to the method of cultivation, and that favorable influences must increase the percentage of individuals with the type of *scintillans* and diminish the percentage of *Lamarckiana*-like specimens.

The self-fertilized seeds of the *cana* individuals previously mentioned have given the following percentages of specimens with the *cana* type: 15 and 16 per cent, 24–34 and 35 per cent, and 46 and 60 per cent, the two latter being found in a culture which excelled the others in vigor. Evidently these figures run parallel to those of *scintillans* and the variability must have the same cause in both cases.

In order to ascertain the nature of this cause I have tried to answer two questions, namely: (1) are the percentage figures

⁷ The mutation theory. Chicago. 1909. pp. 388–391.

different on different parts of the main spike of a plant and on different branches; and (2) are they different for annuals and biennials, provided that the individual strength is in both cases as great as possible? The following experiments will show that the first question is to be answered in the negative, but the second in the affirmative; or in other words, the percentage figures depend upon individual vigor of the plants, and this between the widest possible limits.

The second generation of mutant no. 3, cultivated in 1913, was the most vigorous of all my annual cultures, as already mentioned. I chose for my experiment, therefore, the strongest individual of this group, having the largest supply of pollen in its anthers, and fertilized its flowers on the main spike and on a lateral branch in small bags, each with its own pollen. At the time of harvest I separated the fruits in groups of 10 each; there were 4 of these groups on the main spike and 2 on the branch. In the spring of the following year (1914) I sowed the seeds of these 6 lots separately. I counted the seedlings in the stage shown in fig. 1 without transplanting them. The *cana* were easily distinguished from the *Lamarckiana* by their narrower leaves and gray color. There were a number of dwarfs, which combined with this character those of *cana* and will be called *cana-nanella*. I have planted them out after finishing the countings and found them true dwarfs of the *cana* type. About a dozen of them flowered as annuals, and some flowered the following year as biennials. The result of the countings is given in table III.

TABLE III

	Number of seedlings	Percentage of <i>cana</i>	Percentage of <i>cana-nanella</i>	Percentage together
A, main spike				
base.....	57	40	5	45
second group.....	114	30	4	34
third group.....	121	31	4	35
top.....	129	35	5	40
B, lateral branch				
base.....	95	39	4	43
top.....	94	31	11	42

The means for the whole plant are 34, 6, and 40 per cent. It is easily seen that the deviations from the means fall within the

limits of ordinary chance, although all the seeds from the 10 capsules of each group have been sown. Thus it is clear that the first and the last fruits of a spike and those of a side branch may give the same percentage figures of specimens of the parental type. Moreover, the mean value is not essentially different from the means of the pedigrees, as just given, which was 33 per cent. We may conclude, therefore, that the mean percentage for all my annual cultures is about 30-40.

In order to compare the influence of biennial culture upon this figure, I chose three healthy and very vigorous rosettes of 1913 and kept them through the winter under glass. They had been reared from seeds of a biennial mutant belonging to the group of *cana* mutants from *lata*, from which pedigrees no. 2 and no. 3 were derived; but this special culture stayed in the rosette condition during 1913. In 1914 three plants of the *cana* type became very vigorous, reaching about double the height of the annual plants and growing up to more than 2.5 m. Their stems also had twice the thickness of the others, the foliage and flower spikes were very dense, and the flowers much stouter. Every evening 4 or 5 flowers opened on the same spike, against 1 or 2 in ordinary cases. The number of fruits on a spike was 60-80, whereas 40 fruits, as just given, is a high value for an annual plant. All of these fruits were self-pollinated in little bags, and yielded 1-1.3 cc. of seeds from 10 fruits, whereas the annuals give only 0.5-0.9 cc. of seeds in 10 fruits. We may summarize these details by saying that my biennial specimens of 1914 were about twice as vigorous as the very best of all my annual cultures.

TABLE IV

Plant	Fruits	Seeds in cc.	Seedlings	Percentage of <i>cana</i>
No. 1.	63	6.6	590	96
No. 2.	79	10.0	1099	93
No. 3.	64	6.3	277	97

All the seeds were sown in boxes in 1915 and the seedlings counted out, without being transplanted, in the stage corresponding to fig. 1, when the differentiating marks were very sharp. The three plants gave the results shown in table IV.

The remaining 4-7 and 3 per cent were mostly of the *Lamarckiana* type, with some mutants belonging to *albida*, *oblonga*, and *nanella*. I had saved the fruits and their seeds in 7 or 8 groups, beginning at the base of the spike, and sown the seeds separately. But, just as in the previous case, there were no appreciable differences in the percentage figures between the higher and the lower groups.

The main result is that the percentage of specimens of the *cana* type, which runs 15-60 per cent on annual individuals, may increase to 93-97 per cent on very vigorous biennial plants. It is thus clearly seen to be dependent upon the method of cultivation. Obviously this rule may be applied to the percentages of *O. scintillans*, as previously discussed, and to those of *O. pallescens* and the other new dimorphic mutants to be described in this article.

Oenothera Lamarckiana mut. *pallescens* (fig. 3).—Among all the mutants which arose in my garden from *O. Lamarckiana*, this form most closely resembles the parent type. In early stages the rosettes are the same, and in springtime, when still in the boxes, I have not as yet succeeded in distinguishing them. It is not until about 6 weeks after planting out on the beds that the differentiating marks begin to show (fig. 4). In the middle of June the leaves are clearly shorter, and the blade is set off from the narrowly-winged petiole by a sharp indentation. This character causes the rosettes to be more open because the petioles hardly touch one another.

This spatulate form of the leaves remains, for a long time, the best mark of the race; but when the stem grows up, the whole plant is much more slender than the parent form (fig. 3). The stem is thin and low; in July, when the first flowers open, it often reaches only 75 cm., when the corresponding specimens of *Lamarckiana* are already 1 m. and more in height. After a time, however, this difference disappears, since the spike is more elongated. It is less dense than in *Lamarckiana*; the bracts are much shorter and strikingly broader; the flower buds are large and conical, the flowers somewhat smaller, although still larger than those of *O. biennis*; the pollen is abundant and the fruits are short and thick, containing a good supply of seed. The foliage is of the same green



FIG. 3.—*Oenothera Lamarckiana* mut. *pallescent*: the 2 types into which each generation splits; to the left the *Lamarckiana* type; to the right the parental type; August 1914.

color as in the parent form, but much more crinkled and uneven, not as gray as in *O. cana*, nor as hairy as in this form.

The impossibility of distinguishing the young plants before planting out evidently makes this mutant less fit for the determi-

nation of splitting percentages, because the sorting and counting has to be done on the beds. In my experiments I have always counted the individuals of the two types at the beginning of the flowering period, since at this time the limits between the two groups are the most sharp.

Moreover, this similarity between the mutant and the parent species must diminish the chances of discovering mutant specimens of the new type. This is probably the reason why it was not observed before 1911. Since that year new mutants of the *pallescens* type have more than once arisen from *O. Lamarckiana* and from some of its derivatives,



FIG. 4.—*Oenothera Lamarckiana* mut. *pallescens*: 3 typical leaves of the rosette of radical leaves; June 16, 1914.

especially in 1914. All of these mutants exactly resembled the first one in their whole structure and in all their marks.

I have made pedigree cultures of the offspring of my first three mutants. These arose from seed of the same parent plant of 1909, which belonged to the second generation of a guarded strain of *O. Lamarckiana*, derived from a rosette collected in 1905 in the original field near Hilversum. One part of this seed was sown in 1910 and yielded, among about 500 specimens, 1 *pallescens*, together with 1 *rubrinervis*, 3 *oblonga*, 2 *lata*, 1 *scintillans*, 1 *nanella*, the

specimen of *O. Lamarckiana* mut. *semigigas* described by STOMPS,⁸ and a narrow leaved specimen, exactly resembling the type described and figured by GAGER⁹ for a derivative of *O. biennis*. The specimen of *pallescens* was discovered by chance, since almost none but mutants and a number of doubtful specimens had been planted out; it occurred among the latter and was distinguished as a new type only at the time of flowering. Thereupon, another part of the same sample of seeds was sown in 1911 and yielded two more specimens of *pallescens*, among about 250 flowering individuals.

The self-fertilized seeds of these three mutants gave rise to a mixed progeny, the smaller half of which resembled the parent, whereas the remainder presented the type of *O. Lamarckiana*, duplicating this in all of its special marks and during all the stages of their development. In the following description I will, therefore, indicate them simply as *Lamarckiana*, without discussing the question whether some internal characters might perhaps be different. But externally there is no difference; moreover, the progeny of this derivative *Lamarckiana* behaves exactly like that of normal ones. This splitting into these two types has repeated itself in the following generations and in all of the cases investigated.

Moreover, the *pallescens* seems to be mutable to a higher degree than *O. Lamarckiana* itself; for, although my cultures have been necessarily small, the number of mutants is very striking, reaching 20 among about 500 specimens, or 4 per cent. From the first three mutants I have derived three pedigree families, which I will now briefly describe.

PEDIGREE OF MUT. *pallescens* NO. 1

1910	Mutant	Mutant	
1911, 1913	Second generation	42 per cent <i>pallescens</i>	<i>Lamarckiana</i> 1 mutant <i>rubrinervis</i>
1913	Third generation	23-43 per cent <i>pallescens</i>	<i>Lamarckiana</i> <i>Lamarckiana</i> <i>rubrinervis</i>
1914	Fourth generation	24 per cent <i>pallescens</i>	<i>Lamarckiana</i> <i>Lamarckiana</i>
1915	Fifth generation	38 per cent <i>pallescens</i>	<i>Lamarckiana</i>

⁸ STOMPS, THEO. J., Die Entstehung von *Oenothera gigas* DeVries. Ber. Deutsch. Bot. Gesells. 30:406. 1912.

⁹ GAGER, STUART C., Cryptomeric inheritance in *Onagra*. Contrib. Brooklyn Bot. Garden no. 3, Bull. Torr. Bot. Club 38: 461-471. figs. 2. 1911.

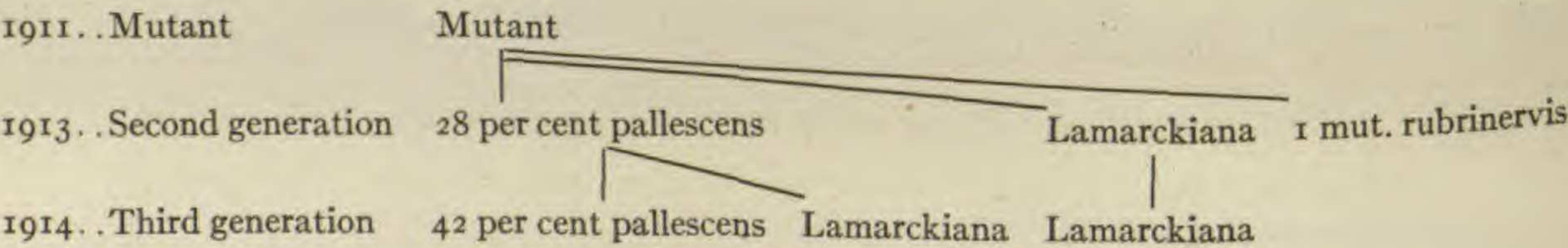
The size of these cultures is given in table V.

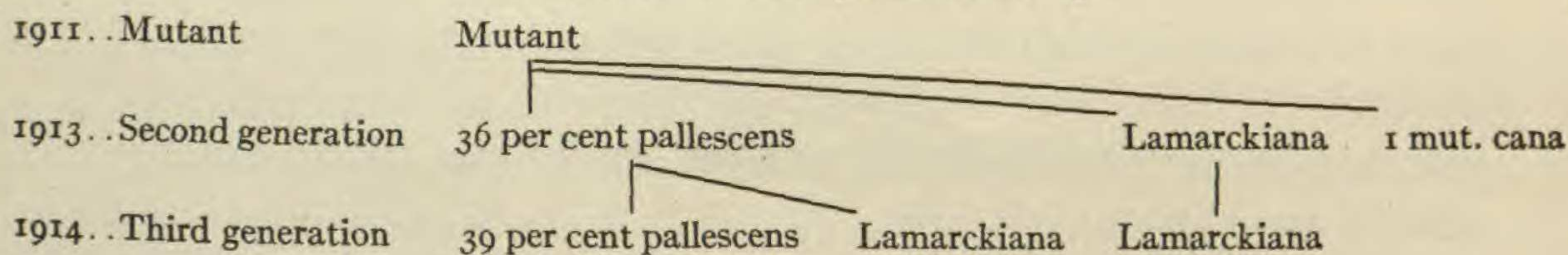
TABLE V

Year	Generation	Parent	Total offspring	Flowering individuals	Percentage of pallescens	Mutants
1911.....	Second	mutant	129	6	1 rubrinervis
1913.....	Second	mutant	40	40	42	1 liquida
1913.....	Third	pallescens	69	69	23
".....	"	pallescens	65	65	43	1 nanella, 1 cana
".....	"	Lamarckiana	90	50	0	1 scintillans, 1 lata, 1 albida
".....	"	Lamarckiana	56	50	0
".....	"	rubrinervis	70	25	0
1914.....	Fourth	pallescens	55	53	24	1 nanella
".....	"	Lamarckiana	58	25	0
".....	"	Lamarckiana	80	25	0
1915.....	Fifth	pallescens	60	25	38

The offspring of the 4 specimens of *Lamarckiana* had this uniform type, in the flowering specimens as well as in the other ones. These were examined in June and July when in large rosettes of radical leaves. The offspring of the mutant *rubrinervis* was also uniform and exactly resembled the race of this name in all its marks, and especially in the brittleness of its stems. The offspring of the original mutant, cultivated in 1911, embraced 129 plants, only 6 of which have flowered, the others having been destroyed before the significance of the culture had been realized. Among these 6, 2 were *Lamarckiana*, 3 *pallescens*, and 1 mut. *rubrinervis*. Their offspring were studied in 1913, as given in table V. Among the mutants the *rubrinervis*, *liquida*, *scintillans*, *lata*, and *cana*, as well as one *nanella*, flowered and proved their identity with the races of these names at that period.

PEDIGREE OF MUT. *pallescens* NO. 2



PEDIGREE OF MUT. *pallescens* NO. 3

The size of these cultures is given in table VI.

TABLE VI

Year	Generation	Parent	Total offspring	Flowering individuals	Percentage of <i>pallescens</i>	Mutants
A						
1911.....	mutant no. 1
1913.....	Second	mutant	25	25	28	1 <i>rubrinervis</i>
1914.....	Third	<i>pallescens</i>	57	57	42	5 <i>nanella</i>
1914.....	Third	Lamarckiana	60	25	0
B						
1911.....	mutant no. 2
1913.....	Second	mutant	25	25	36	1 <i>cana</i>
1914.....	Third	<i>pallescens</i>	25	25	39	1 <i>lata</i> , 3 <i>nanella</i> , 1 <i>cana</i>
1914.....	Third	Lamarckiana	65	25	0

Among the mutants the *rubrinervis*, both *cana*, one *lata*, and some *nanella* have flowered. The individuals of *pallescens* and *Lamarckiana*, which did not flower, were examined in June and July as large rosettes. Most of the flowering specimens were observed during the months of August and September.

The percentage figures of these tables vary from 23 to 43, the means for the 3 families being 33, 35, and 37 per cent, and the total mean being 35 per cent. On account of the evident weakness of the individuals of the *pallescens* type, as compared with their *Lamarckiana*-like sisters, these figures may be assumed to show that the splitting into two main types took place in about equal parts. The splitting is constantly repeated from the *pallescens* specimens, but the progeny of the *Lamarckiana* type retain this type uniformly.

I have made only one cross in these families, and that in order to ascertain the properties of the pollen of the *pallescens* individuals. I placed this pollen on the stigma of some flowers of

Lamarckiana in 1913, and got from the seeds a uniform generation of 60 flowering individuals, all of which proved to be *Lamarckiana*. I conclude from this fact that the pollen of the *pallescens* plants does not transmit the characters of the race, exactly as in *O. scintillans* and *O. cana*.

O. Lamarckiana lata mut. *Lactuca* (fig. 5, C).—In the summer of 1913 I found, in a race of *O. lata* which had been fertilized in the



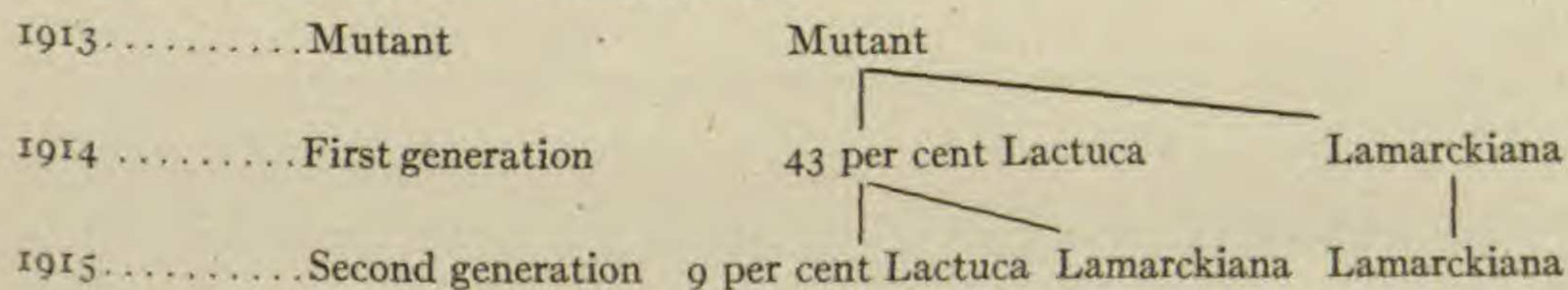
FIG. 5.—Typical radical leaves of A, *Oenothera Lamarckiana* mut. *liquida*; B, mut. *cana*; C, mut. *Lactuca*; June 1914.

previous generations (1905 and 1907) by *O. Lamarckiana*, a weak plant which seemed to be new to me, but showed evident signs of affinity with the inconstant types of *O. cana* and *O. pallescens* as previously described. It was fertilized, therefore, purely by its own pollen. It yielded 0.8 cc. of seeds, which were sown in 1914 and gave rise to 65 plants, one of which was a mutant of the ordinary type of *O. nanella*, and subjected to the same bacterial disease which so often deforms the dwarfs of my race. Among

the others, two types were represented in about equal numbers. One type was exactly like normal *Lamarckiana*; it counted 36 individuals, almost all of which have flowered, without showing any recognizable difference from the original wild species. The remaining 28 constituted a new and uniform type, repeating the characters of the parent plant of 1913, so far as these had been noticed and recorded. At the time of planting out, in the beginning of May, they very much resembled the compact rosettes of *O. nanella*, but without any signs of the disease. About the middle of June, when the rosettes of the type of *Lamarckiana* were growing very fast, those of the new

type remained small, their leaves reaching only about half the length and half the breadth of those of their sisters (7×3 cm. against 14×5 cm.). Their blades were sharply set off from the winged petioles (fig. 5, C), and thereby they much resembled those of *O. pallescens* (fig. 4). This resemblance continued during the development of the stem and the flower spikes; but even as the rosettes were smaller and more densely leaved, the stems were lower and weaker and less branched. The leaves were narrower and folded along the middle vein, instead of being broad and flattened, as in *O. pallescens*. The flower buds were as thick and as large as those of this species, and the flowers also reached the same size, the petals having a length of 4 cm. During the flowering period the differences from *O. pallescens* grew gradually less, and at the end, in September, the new type seemed to be only a weak form of this latter, reaching a less height and being almost unbranched. Artificial self-fertilization has been difficult, since in many flowers the pollen was in an imperfect condition. Four specimens yielded a sufficient harvest (0.5–1 cc.). The sister plants of the *Lamarckiana* type showed an abundance of seed, exactly as the *Lamarckiana* of pure origin does.

The next year (1915) I sowed the seeds of one specimen of the parental type and of two of the type of *Lamarckiana*. The first gave only 44 seedlings, of which 4 were *Lactuca*, one *nana*, and the others *Lamarckiana*. The two other sowings gave 248 and 283 offspring of their own type, without any *Lactuca* specimens, but with some dwarfs. The number of them was 11, or 4 per cent in the first group, but only one in the latter group. Combining these results we get the following pedigree:



Although only two generations from the seeds of the original mutant have been cultivated, it is evident that this new form behaves exactly like the inconstant races of *O. scintillans*, *O. cana*, and *O. pallescens*. Under favorable conditions it splits into about

equal numbers of the mutant type and of the type of *O. Lamarckiana*. Moreover, a mutant dwarf has been produced.

O. Lamarckiana mut. *liquida* (fig. 5, A).—In 1912 and 1913 a new type of mutant was discovered, which came next to *O. scintillans*, had flat and smooth leaves like that form, but the foliage was much broader and lighter green. The individual mutants resembled one another in all respects, save the size of the flowers; they were very slender and had leaves about two-thirds the size of those of *O. Lamarckiana*. The pollen was sometimes abundant, but in other flowers rather scanty.

All in all, I had 6 mutants of this type. One came from seed of *O. Lamarckiana*, but unfortunately it failed to produce good seeds, although the fruits were well developed. Four others arose from *O. lata* × *Lamarckiana*, two in 1912, which also did not yield fertile seeds, and two in 1913. The last one was found in the culture of *O. pallescens* mut. no. 1, and mentioned previously. The seeds of the 3 fertile mutants were sown in 1914 and yielded small cultures, which split up into two types, one repeating the mutant parents in all respects, and the other differing in no visible way from ordinary *O. Lamarckiana*. Besides these there were some mutants which happened to belong to allied types. Table VII gives the size and constitution of these cultures.

TABLE VII
SECOND GENERATION OF *O. liquida*

Mutant 1913 from	Lamarckiana	liquida	Mutant	Total	Percentage of liquida
pallescens	11	6	17	35
lata	61	26	1	88	30
lata	13	8	2	23	35
Total	85	40	3	128	31

In each of these cultures 15 individuals have been allowed to flower, about one-half of these being the *liquida* type and the other half the *Lamarckiana* type. The 3 mutants were *scintillans*, *pallescens*, and *cana*. All 3 have grown vigorously and flowered in August and September; they differed in no respect from the races of the same names.

The percentage of typical individuals in the second generation is about the same as for *O. cana* (25 and 53 per cent), for *O. pallescens* (35 per cent), and for *O. Lactuca* (43 per cent). From this it may be concluded that the 4 races have the same hereditary constitution which, moreover, is the same as in *O. scintillans*.

The next year (1915) I cultivated a third generation of the second mutant of the table (mutant no. 1 from *lata*). The harvest had been small, as in the previous generation, and only 33 seeds germinated. Of these 9 were *liquida*, 1 was *pallescens*, 1 *oblonga*, and the others *Lamarckiana*. All of them have flowered. The percentage for *liquida* was 27, or about the same as in the first generation. Moreover, I have sown for each of the 3 cultures of 1914 the seeds of one or two typical individuals, and also for each of them the seeds of two of the atavistic or *Lamarckiana* type. These 6 last sowings contained 150–300 seedlings each, together 1311, of which 8 were mutants (3 *oblonga*, 4 *lata*, 1 *cana*); the remainder were all of the *Lamarckiana* type, no *liquida* occurring among them. The seedlings of the 4 *liquida* specimens gave the results indicated in table VIII.

TABLE VIII

THIRD GENERATION OF *O. MUT. liquida*

Race issued from	Total of seedlings	Percentage of <i>liquida</i>
<i>pallescens</i>	84	25
<i>pallescens</i>	47	28
<i>lata</i> no. 1	80	41
<i>lata</i> no. 2	26	35
Total	237	32

The countings were made in June and July in the boxes in which the seeds had been sown; the plants were all young rosettes with leaves 15 cm. long in the *Lamarckiana* type, and 6–10 cm. long in the *liquida* specimens. The differences were clear and sharp. The table shows that the splitting was almost exactly the same in the third as in the second generation.

Dimorphic races do not seem to be rare among the mutants of *O. Lamarckiana*, and have been observed to spring also from its

hybrids with other species; but the characters are not always as sharp as in the instances described, or the production of seeds is too insufficient for further cultures. Only one case may still be mentioned here. It was a mutant from *O. lata*, discovered in 1914, the self-fertilized seeds of which gave a dimorphic second generation, consisting of 19 plants of the parental type, 47 of the *Lamarckiana* type, besides 2 mut. *oblonga* and 2 mut. *lata*. Almost all of these flowered in 1915. Those of the parental type were strikingly like one another, constituting a wholly new form, with very long, narrow, dark green leaves, the stems low and scarcely branching, the spikes rich with bright flowers like those of *Lamarckiana*, and with a good supply of pollen. The fruits, however, were cylindrical and very thin, containing only a few good seeds. The plants excelled in beauty the species and most of its other mutants, but on account of its slight fertility I do not propose to continue the culture. It may be called *O. superflua*.

O. biennis Chicago mut. *saligna*.—In the second generation of my race of *O. biennis Chicago*¹⁰ I found in 1913, among 870 normal individuals, two specimens of a weaker, narrow-leaved type, which differed sufficiently from the former mutants of this species, namely, from *O. biennis Chicago* mut. *salicifolia* and mut. *salicastrum*,¹¹ to be considered a new form. One of these new mutants died before flowering, the other yielded, after self-fertilization, a small but sufficient harvest of seeds. One-half of these seeds were sown, but only 17 specimens germinated and grew up into flowering plants. Of these 9 repeated the type of the parent, but 8 returned to the size, vigor, and characters of *O. biennis Chicago*, the grandparent. Although the numbers are very small, they point to a splitting into equal parts, as in the splitting mutants of *O. Lamarckiana* just described.

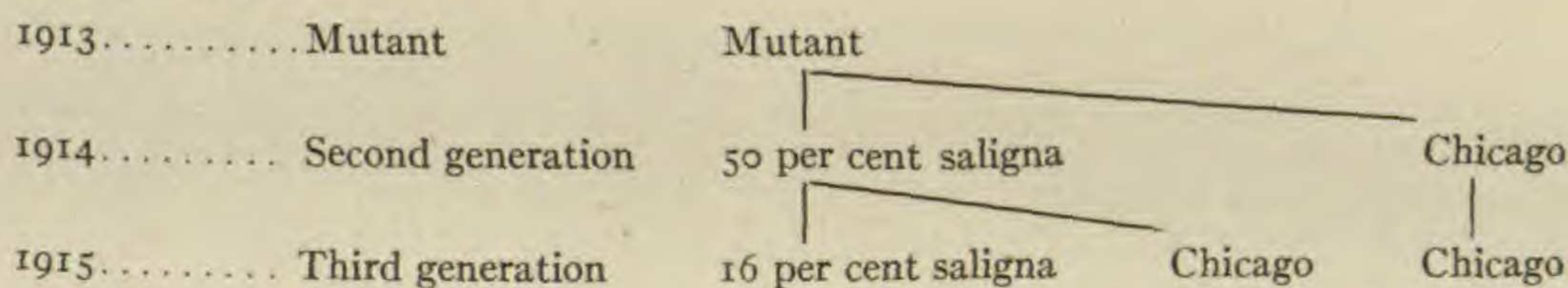
The difference was already evident in March, when the seedlings were only two months old. In June the rosettes were large, but smaller than those of the species, the leaves smooth and narrow. The stems grew up to about one-half the height of their atavistic sisters, and began to flower in September, having a length of 60–120

¹⁰ Gruppenweise Artbildung, pp. 34, 52, etc. 1913.

¹¹ Gruppenweise Artbildung, p. 304. figs. 110, 111.

cm. The spikes were densely flowered, the flowers a little smaller, the fruits thin and long. The production of pollen was insufficient in many flowers, but this may have been the effect of the individuals being transplanted from their boxes to the bed in June, which is relatively late in the season. The seed developed badly and contained only a small percentage of normal grains.

I have sown the seeds of 8 of the 9 specimens with the parental type, and of two of the type of *O. biennis Chicago*. The first split into two types, the second only repeated the form of the parent. The splitting percentages were 11, 12, 13, 15, 15, 17, 18, and 25, with a mean of 16 per cent, but the germination had been very poor, giving only 444 seedlings for the 8 boxes. The progeny of the two specimens of the *Chicago* type was uniform with 252 and 60 seedlings. I counted them in May and June, and left one group of each type to flower. The group from the *saligna* type contained two flowering *saligna*, identical with those of the second generation; that of the atavists 60 flowering plants of the uniform type of *O. biennis Chicago*. From these facts we may conclude that in this race all of the specimens of the parental type give a dimorphic progeny, while the offspring of the plants with an atavistic type remains uniformly so. Resuming the cultures, we get the following pedigree:



The behavior is exactly the same as in the dimorphic races issued from *O. Lamarckiana*.

Crosses of *Oenothera Lamarckiana* mut. *cana*.—As indicated on p. 258 I chose in 1913 the second generation of a *cana* mutant which arose from *O. lata* (no. 3) for a series of crosses. This culture was the most vigorous one of all my annual *cana* families, and its percentage figures seemed to be more normal than in the other cases. The crosses were made in both directions with the pure strains of my species and races described in *Gruppenweise Artbildung*, and the seeds were sown in 1914. This first generation

was counted in July, during the beginning of the flowering period, but about one-half of some of the cultures were kept in the boxes so as to reach only the stage of rosettes at that time. No second generations have been cultivated. I will first describe the results, and afterwards give the necessary details concerning the several cultures.

The main purpose of these crosses was to decide the question whether the special characters of *O. cana* are handed down by the ovules only, as in *O. scintillans* and *O. lata*, or by the pollen also. Table IX gives the result of the crosses with wild species other than *O. Lamarckiana*. Here a splitting occurs into *laeta* and *velutina* or into *densa* and *laxa*, exactly analogous to that produced by *O. Lamarckiana* itself. The only exception is the pollen of *O. biennis*, which does not split; it gives with *O. cana* the same type as with the parent species. The result was very striking on the beds. No specimens of the *cana* type occurred in the cases where this mutant had been the father, whereas such individuals abounded in the results of the reciprocal crosses.

TABLE IX
CROSSES OF *O. cana* WITH OTHER SPECIES

Cross	Percentage of cana	Percentage of laeta	Percentage of velutina	Percentage of mutants
A				
<i>O. cana</i> × <i>O. biennis</i> Chicago	25	11	63	1
<i>O. cana</i> × <i>O. Cockerelli</i>	17	17	63	3
<i>O. cana</i> × <i>O. Hookeri</i>	28	14	58
<i>O. Hookeri</i> × <i>O. cana</i>	0	4	96
<i>O. Cockerelli</i> × <i>O. cana</i>	0	54	46
<i>O. syrticola</i> × <i>O. cana</i>	0	51	49
<i>O. biennis</i> × <i>O. cana</i>	0	58	42
B				
		Percentage of densa	Percentage of laxa	
<i>O. biennis</i> Chicago × <i>O. cana</i>	0	24	75	1
<i>O. atrovirens</i> × <i>O. cana</i>	0	36	64
C				
<i>O. cana</i> × <i>O. biennis</i>	49	51	

In this table, *O. syrticola* Bartlett is the *O. muricata* L. of my *Gruppenweise Artbildung*, and *O. atrovirens* Bartlett has been

described in that book as *O. cruciata* Nutt. The other names are still the same as in my book.

With the same purpose crosses were made with *O. Lamarckiana* and some of its derivatives.

TABLE X

CROSSES OF *O. cana* WITH *O. Lamarckiana* AND ITS MUTANTS

Crosses	Percentage of <i>cana</i>	Percentage of <i>Lamarckiana</i>	Percentage of other forms
<i>O. cana</i> × <i>O. Lamarckiana</i>	42	58
<i>O. cana</i> × <i>O. nanella</i>	21	71	8 nanella
<i>O. cana</i> × <i>O. rubrinervis</i>	40	25	35 subrobusta
<i>O. Lamarckiana</i> × <i>O. cana</i>	0	98	2 nanella
<i>O. lata</i> × <i>O. cana</i>	1	62	35 lata, 3 mutants
<i>O. nanella</i> × <i>O. cana</i>	1	5	94 nanella
<i>O. oblonga</i> × <i>O. cana</i>	0	82	15 oblonga, 3 mutants
<i>O. rubrinervis</i> × <i>O. cana</i>	0	52	48 subrobusta

The main result is the same. *In all the crosses of both tables the characters of O. cana are handed down through the ovules to a large part of the progeny, but not through the pollen.* The behavior is exactly the same as in *O. scintillans* and *O. lata*. The two specimens of *O. cana* from the crosses of *O. lata* and *O. nanella* must evidently be considered as mutants, that is, as having arisen from the fertilization of mutated sexual cells, since we have seen that such mutations occur from time to time, especially among the seeds of *O. lata*.

Apart from the appearance of plants of the *cana* type, the results of the crosses are, in every case, such as would be expected if *O. Lamarckiana* had been used instead of *O. cana*. In this respect they simply confirm the conclusions given in my book.

Let us now consider in its details the analogy of *O. cana* with the allied forms of *O. scintillans* and *O. lata*. Two cases offer themselves for this consideration. The first one is afforded by the crosses with *O. biennis*. Apart from stray mutants, these produce two types, one of which combines the visible marks of both parents, whereas the other wholly lacks the characters of the mother, but is simply like the hybrid of *O. Lamarckiana* and *O. biennis*, as described in my book. In the first group the combination is such as to make the characters of the mother the most

striking in the hybrids, whereas those of the father, *O. biennis*, have only a less influence on the general type.

In table XI the figures of table IX are combined with the percentages derived from my *Gruppenweise Artbildung*, by taking the means of the two crosses for each case given on pp. 251 and 261.

TABLE XI

O. cana × *O. biennis* COMPARED WITH *O. lata* AND *O. scintillans*

Forms	Percentage of type of mother	Percentage of type of <i>O. Lamarckiana</i> × <i>O. biennis</i>	Mutants
<i>O. cana</i> × <i>O. biennis</i>	49	51
<i>O. scintillans</i> × <i>O. biennis</i>	60	36	4
<i>O. lata</i> × <i>O. biennis</i>	57	43
Mean.....	55	43

In this table we see that the characters of *O. cana*, even as those of *O. scintillans* and *O. lata*, are repeated in about one-half of the progeny, but not in the other half. We may consider this as the simplest case. In the other crosses the proportions of *cana* are 17, 25, 28, with a mean of 23 per cent in table IX, and 21, 40, 42, mean 34 per cent in table X, and these figures may be assumed to point to a splitting into nearly equal parts with a loss on the side of the weaker form. Exactly the same behavior occurred among the progeny of the self-fertilized individuals of *O. cana*, as we have seen previously.

Let us now compare *O. cana* with the two allied forms in those crosses where the progeny splits into the twin hybrids *O. laeta* and *O. velutina*, as shown in table XII.

The types of *O. laeta* and *O. velutina* have been compared in each case with the twins derived from *O. Lamarckiana* by the same father.¹² The comparison embraced the whole lifetime from the germination in February until the production of the fruits in September. No differences have been observed.

From table XII we see that the splitting percentages are practically the same, whether the pollen is taken from *O. biennis* Chicago, *O. Cockerelli*, or *O. Hookeri*. For this reason I have given

¹² DEVRIES, HUGO, On twin hybrids. BOT. GAZ. 44:401-407. 1907.

the mean for each group in the last columns of the table, and the reliability of this mean evidently depends strongly on this fact.

TABLE XII
SPLITTING INTO *laeta* AND *velutina*

FORMS	PERCENT- AGE OF TYPE OF MOTHER	PERCENT- AGE OF LAETA	PERCENT- AGE OF VELUTINA	MEANS FOR THE GROUPS		
				Type of mother	laeta	velutina
O. cana × O. b. Chicago . . .	25	11	63	} 23	14	61
O. cana × O. Cockerelli . . .	17	17	63			
O. cana × O. Hookeri	28	14	58			
O. scintill. × O. b. Chicago .	33	32	32	} 30	36	30
O. scintill. × O. Cockerelli .	21	49	29			
O. scintill. × O. Hookeri . . .	35	28	29			
O. lata × O. b. Chicago	21	24	55	} 27	25	46
O. lata × O. Cockerelli	21	31	48			
O. lata × O. Hookeri	39	18	43			
O. Lamarckiana × O. b. Chicago		19	81	}	18	82
O. Lamarckiana × O. Cock- erelli		11	89			
O. Lamarckiana × O. Hook- eri		23	77			
O. nanella × O. b. Chicago		41	59	}	41	59
O. nanella × O. Cockerelli		38	62			
O. nanella × O. Hookeri		45	55			

Theoretically a splitting into 4 groups of equal size should be expected, namely into *cana-laeta*, *cana-velutina*, *laeta*, and *velutina*.¹³ Evidently one of the first two groups is suppressed. This conclusion holds good for *O. cana* just as for *O. scintillans*, but in the case of *O. lata* the fourth group is sometimes visible, a few specimens of the *lata*-like hybrids assuming at the same time the marks of *O. laeta* (about 1 per cent, *Gruppenweise Artbildung*, p. 255), whereas the remainder are clearly *lata-velutina*. It is probable that the same group is suppressed in both the other cases, and for the same reasons, which are as yet unknown. The fact that there are so often more *velutina* than should be expected probably has the same cause as the exuberant occurrence of this form in the crosses of *O. Lamarckiana* (82 per cent). The analogous crosses of *O. nanella*, given in the lower part of the table, show that these

¹³DE VRIES, HUGO, On triple hybrids. BOT. GAZ. 47:1-8. 1909.

diminutions of the *laeta* type may, at least in part, be considered as influenced by neighboring characters. The combination *O. cana nanella* has occurred in many instances during these experiments, either from the crosses of *O. cana* with the dwarfs of my race, or as occasional mutations in other cases. A repetition of my experiments, in which *O. cana nanella* would be chosen for fertilization by the other species or mutants used, would probably give the material to decide these questions.

Putting aside all of these more special considerations, we may conclude that *O. cana* behaves in its crosses, as well as after self-fertilization, exactly after the manner of *O. scintillans* and *O. lata*. From this fact and from the cross *Lamarckiana* × *palleszens*, previously mentioned, it seems probable that the other new dimorphic mutants, namely *O. pallescens*, *O. liquida*, and *O. Lactuca*, will follow the same rule if tried in the same way. This rule is evidently independent of the external types of their characters, but must depend upon internal properties of their hereditary qualities.¹⁴

I will now give briefly the necessary details concerning the crosses mentioned in tables IX and X. As already mentioned, all these crosses were made in 1913 with plants of the same origin. For every cross a single specimen was chosen and some flowers on the lower part of its main spike were castrated. The seeds were sown in February 1914, the seedlings transplanted into boxes, and from these, as a rule, about 25 specimens of each culture were placed in a bed in April and May, giving them a good soil and light exposure and plenty of space to insure a vigorous development until the time of flowering and of fruiting.

O. cana × *O. biennis* Chicago.—A group of 71 specimens, all of which produced high stems and 25 of which have flowered. One was a mutant, combining the gray narrow leaves of *O. cana* with the marks of the stature, foliage, and flowers of *O. lata*. The plants of the type of *O. cana* were exactly like pure *O. cana* at the beginning of the flowering period, in July, when they had reached a height of 70 cm. The remaining plants were like (*O. Lamarckiana* × *O. biennis* Chicago) *laeta* and *velutina*. The reciprocal cross yielded 59 specimens, of which 5 remained in the condition

¹⁴ On these questions see Gruppenweise Artbildung, pp. 268–295. 1913.

of rosettes. Of the remaining 54, about one-half or 25 have flowered, the others reaching this stage approximately at the time when they were pulled up and counted. One plant was a mutant, being a metaclinous *velutina*, just as described in my book on pp. 308-311. The others were *densa* and *laxa*, as should be expected, and agreeing with these types throughout their whole life.

O. cana × *O. Cockerelli*.—A culture of 63 specimens embracing 4 *cana*, 5 *laeta*, and 15 *velutina*, which have flowered, and a large number of rosettes of radical leaves. Two plants were mutants of the type of *O. lata* and one of them has flowered. Neither in the rosette stage nor at the time of flowering have the plants of the *cana* type showed any difference from ordinary *O. cana*, the characters of the father, also of its twin hybrid type, being invisible in them. Such was the case in almost all the beds containing the hybrids whose mother was *cana*, and this made the distinguishing and counting of this type quite easy and sharply defined, and therefore fully reliable. Short narrow leaves of a gray color, a slender spike with long, thin flower buds with nodding tips were everywhere the same distinguishing marks. The *laeta* and *velutina* had the ordinary type of these twins, as produced by *O. Cockerelli*.

The reciprocal cross yielded 19 annual and 13 biennial *laeta*, besides 4 annual and 23 biennial *velutina* of the same type. The annual plants have flowered; the biennials became stout rosettes in July and August.

O. cana × *O. Hookeri*.—Represented by 25 flowering plants, 3 younger ones, and 40 rosettes, and among the flowering individuals 5 *cana*, 5 *laeta*, and 4 *velutina*. The *cana* were like those of the pure type; the *laeta* and *velutina* did not differ from those of the cross *O. Lamarckiana* × *O. Hookeri*, some of the *velutina* being of a yellowish green in such a degree as not to be able to produce a stem. The reciprocal cross yielded only two *laeta*, one of which has flowered, among a culture of 60 specimens. The remainder were *velutina*, 24 flowering plants and 34 rosettes of radical leaves. The types were the same as those in the reciprocal cross.

O. syrticola × *O. cana*.—Represented by 60 specimens of the type of (*O. syrticola* × *Lamarckiana*) *laeta* and *velutina*. Of these 19 *laeta* and 6 *velutina* have flowered, reaching a height of 2 m. in

August. The remaining plants were pulled out as large rosettes in July.

O. atrovirens × *O. cana*.—Represented by 55 plants, among which 8 *densa* and 17 *laxa* have flowered. They were in all respects like the twins of the corresponding cross of *O. Lamarckiana*. Just as in this cross, some specimens had cordate petals and others had linear ones, repeating the *cruciata* type. But on the first plants stray flowers with narrower petals were found, from time to time, indicating a high degree of fluctuability rather than a splitting into two constant and uniform types.

The reciprocal cross yielded only 23 seedlings, 20 of which were yellow and died very early, and the 3 remaining ones were very weak, reaching only a height of 40–60 cm. when they flowered. They had the type of the *gracilis* of the corresponding cross of *O. Lamarckiana*. They were not mentioned in table IX.

O. cana × *O. biennis* L.—Among 70 plants of this culture, one-half had the type of *O. Lamarckiana* × *biennis*, and of these 15 have flowered. The other half were evidently *cana*. Of these, 28 had the stature of typical *O. cana*, but with some marks which indicated an influence of the father. The foliage was less gray, a darker green, with broader bracts, and more dense spikes with smaller flowers than in the other crosses. The stigmas were surrounded by the anthers, insuring natural self-fertilization, as in *O. biennis*. Besides these intermediate types there were 7 dwarfs, which had the gray, narrow, and pointed foliage of *O. cana*, and which in the table have been calculated together with the high specimens of the *cana* type.

The reciprocal cross yielded only *laeta* and *velutina*, together 57 plants, of which about one-half of each type have flowered.

O. cana × *O. Lamarckiana*.—The two types of this culture were exactly the same as in the self-fertilized offspring of the mutant. There were only 19 specimens, of which 6 were *cana*, 11 *Lamarckiana*, and 2 *nanella*. The dwarfs combined the marks of *cana* with those of *nanella* and have been calculated in the table with the *cana* specimens of tall stature.

The same cross had been made in 1907, the seeds being sown in 1913. In this case there were 50 offspring, among which 26

were *cana* and 23 were *Lamarckiana*, while one dwarf occurred. The percentage figures, 52 *cana* and 46 *Lamarckiana*, confirm those of table X.

The reciprocal cross yielded only normal *Lamarckiana*, 60 specimens with one dwarf. Of these 23 have flowered.

O. lata × *O. cana*.—In this case the differences were already very clear at the beginning of June. There were 34 *lata*, 61 *Lamarckiana*, and 3 mutants (one each of *cana*, *nanella*, and *oblonga*). In August 7 *lata* and 9 *Lamarckiana* flowered. They repeated the type of the hybrids of *O. lata* with the parent species.

O. cana × *O. nanella*.—Only 24 seeds germinated. These produced 5 *cana*, 17 *Lamarckiana*, and 2 dwarfs which had the characteristics of *O. cana*. All these plants have flowered.

The reciprocal cross gave 111 plants, of which one was a *cana* of normal stature, 105 were *cana* with the dwarfish stature of *O. nanella*, and 5 had the type of *O. Lamarckiana*. Two of this last type, the normal specimen of *cana*, and 22 dwarfs flowered in August.

O. oblonga × *O. cana*.—Already in June the differences were clear and unmistakable. Among 72 plants 59 were of the *Lamarckiana* type, 11 *oblonga*, 1 *albida*, and 1 *rubrinervis*. Of these, 2 *oblonga* and 12 *Lamarckiana* flowered; most of the others lived through the summer in the condition of large rosettes of radical leaves.

O. cana × *O. rubrinervis*.—Only 20 seeds germinated, and yielded 8 *cana* of the normal type, 5 *Lamarckiana*, and 7 *subrobusta*, all of which have flowered.

The reciprocal cross yielded 59 plants, but in only two types, which were the same as those in the first instance. Of these, 17 *Lamarckiana* and 8 *subrobusta* have flowered.

Summary

1. Besides *O. scintillans*, which splits under ordinary circumstances in every generation into nearly equal groups of plants of the same type and others of the type of *O. Lamarckiana*, I have cultivated pedigree families of 4 other mutants of *O. Lamarckiana* which behave in the same manner. They have been designated

as *O. cana*, *O. pallescens*, *O. Lactuca*, and *O. liquida*. Their *Lamarckiana*-like offspring are constant in their progeny. Besides the two main types, they produce, as a rule, a relatively high percentage of other mutants.

2. The specimens of the parental type are on the average produced in about 40 per cent, the other 60 per cent being *Lamarckiana* with some mutants; but these figures vary with the cultures and with the plants according to their individual strength. They may even increase, on very strong biennials, to 93–97 per cent for the parental type.

3. Dimorphic mutants of this type occur also in allied species of the *biennis* group, as has been discovered by BARTLETT in the case of *O. stenomeres* mut. *lasiopetala* and described in this article for *O. biennis* *Chicago* mut. *saligna*.

4. In the crosses with older species or with *O. Lamarckiana* and its derivatives, *O. cana* follows exactly the type of the analogous crosses of *O. scintillans* and *O. lata*.

5. In the dimorphic mutants, the special characters are handed down to the next generation through the ovules only. The pollen lacks these characters, and is, so far as investigated, not different from that of pure *O. Lamarckiana*.

6. The dimorphic mutants constitute a group in which the hereditary phenomena are evidently independent of the externally visible characters of the special members of the group, but must be assumed to have the same intrinsic causes in the different cases.

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